

## Temporal and Spatial Patterns in Abundance and Diversity of Fish Assemblages in Elkhorn Slough, California

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**ABSTRACT:** Assemblages of ichthyofauna of shallow inshore habitats along California's central coast are described in terms of species composition, abundance, and life-style categories. A total of 22,334 fishes from 65 species and 27 families was collected with otter trawls at six sites in the main channel and tidal creeks of Elkhorn Slough, a tidal embayment and seasonal estuary, and two nearshore ocean stations in Monterey Bay during 44 months between August 1974 and June 1980. Greater than 90% of the catch comprised 10 species. The four dominant species, *Cymatogaster aggregata*, *Leptocottus armatus*, *Phanerodon furcatus*, and *Embiotoca jacksoni*, occurred during most or all seasons and were classified as residents or partial residents. Several abundant species were marine immigrants that seasonally use the slough as spawning and nursery grounds; this resulted in higher abundance and species richness during summer. Species collected during winter largely were slough residents. Species composition and richness varied with distance from the slough entrance. The ocean assemblage was most different, and its similarity to other stations decreased progressively with distance inland and into the tidal creeks. During our study, 5,074 fishes were collected by beach seine in Bennett Slough, a remote shallow marsh basin adjacent to the entrance of Elkhorn Slough. Species richness was relatively low and three euryhaline species accounted for >80% of the total catch. The species assemblage was most similar to those at the tidal creek and most shallow stations of Elkhorn Slough. Resident species numerically dominated assemblages in Bennett Slough and the most inland areas of Elkhorn Slough. The high relative abundance of marine-related fishes (classified as marine, marine immigrant, and partial resident) entering Elkhorn Slough early in life or as spawning adults indicates the importance of this habitat to nearshore fish assemblages.

### Introduction

Shallow bays and estuaries are recognized worldwide as productive habitats used by a variety of fishes for reproduction, feeding, and shelter (Odum and Heald 1975; Dando 1984; Day and Yanez-Arancibia 1985, among others). These systems function as important nursery grounds for larval and juvenile stages of many marine fishes, potentially enhancing their early growth and survival (Allen 1982; Rosenberg 1982; Weinstein 1985). This nursery function often has been discussed in terms of the estuarine dependence of marine species. More broadly, estuarine dependence includes any species using estuaries as essential habitat during any life history stage (Blaber et al. 1989). Those species regularly entering estuaries to spawn or

feed, as well as those completing their entire life cycle in the area, also can be considered to be dependent on estuarine systems.

Because most species are not dependent entirely on estuaries and are found also in adjacent coastal environments, Lenanton and Potter (1987) suggested the term "estuarine opportunism." Although difficult to evaluate because it requires seasonal sampling over several years in all major habitats of the estuary and adjacent marine area, the benefits derived by opportunistic members of the estuarine fish assemblage would be a measure of the interaction between estuarine and coastal marine environments (Darnell and Soniat 1979; Weinstein 1981). Identifying this inshore-offshore relationship is important to maintaining all coastal resources.

The functional relationship between estuaries and fish communities has been studied widely along the east coast of the United States, particularly in expansive tidal marshes (Shenker and Dean 1979;

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Weinstein 1979; Bozeman and Dean 1980). Although estuaries represent only 10–25% of the west coast, compared to 80–90% of the Atlantic and Gulf of Mexico coasts (Day and Yanez-Arancibia 1985), they have been identified as important nursery and spawning areas for some commercially valuable marine fishes (Pearcy and Myers 1974; Krygier and Pearcy 1986; McGowan 1986; Gunderson et al. 1990). Bays and estuaries of California, in particular, are few in number and size; their total area is less than 15% that of Chesapeake Bay (Horn and Allen 1976). In addition, more than 75% of California's coastal wetlands have been lost or degraded through pollution, diking, and filling (Onuf et al. 1978). Nonetheless, unique assemblages of fishes using those remaining coastal systems contribute to California's nearshore marine resources (Allen 1982; Horn and Allen 1985).

Fish assemblages of Elkhorn Slough, a primarily marine-influenced wetland habitat on the central California coast, have been studied since the mid-1970s by faculty and graduate students of Moss Landing Marine Laboratories (California State University system). These investigations provide valuable information on life histories, abundance, and distribution of fishes throughout this system, including tidal creeks and adjacent Bennett Slough and marine coastal habitats (Ambrose 1976; Appiah 1977; Cailliet et al. 1977; Antrim 1981; Barry and Cailliet 1981; Yoklavich 1982; Barry 1983). Further interest has been stimulated by the recent designation of Elkhorn Slough as a member of the National Estuarine Research Reserve System and as the site of marsh restoration projects. Using data that were collected regularly during four years, the objectives of the present study were (1) to assess seasonal and spatial changes in species composition, abundance, and habitat associations of fish assemblages in Elkhorn Slough; and (2) to evaluate the interaction between fish assemblages in the slough and those in adjacent nearshore ocean habitat, especially in terms of "slough dependence or opportunism." This study provides baseline information prerequisite to long-term monitoring of fish assemblages in Elkhorn Slough, their response to potential environmental changes (both naturally and human-induced), and their contribution to the nearshore fishery resources of Monterey Bay.

## Methods

### STUDY AREA

Elkhorn Slough (36°48'N, 121°47'W) is a shallow, tidal embayment and seasonal estuary at the head of the Monterey submarine canyon. It has an axial length of about 10 km and a relatively small drainage basin of 585 km<sup>2</sup> (Fig. 1; Browning 1972).

During our study, water depth of the main channel below mean lower low water (MLLW) ranged from about 5 m at the slough entrance to less than 2 m at the most inland station; average width of the main channel narrowed from 100 m at the entrance to 15 m furthest inland (Smith 1973; Broenkow 1977). The main channel is bordered by extensive mudflats (about 170 ha are exposed at MLLW) and is intersected by a network of tidal creeks that meander through adjacent salt marshes (about 583 ha comprised predominantly of pickleweed [*Salicornia virginica*]).

Our study area included several sites along the main channel of the slough, from the entrance to Hudson's Landing (Fig. 1). In addition, we sampled Long Canyon, a tidal creek that is 1–1.5 km long, 5–10 m wide and 2 m deep at its intersection with the main channel (about 4 km east of Moss Landing Harbor entrance), and receives freshwater runoff from the adjacent watershed. We also sampled Rubis Creek (Fig. 1), which intersects the main channel across from Long Canyon Creek and is about the same width and depth but receives little freshwater runoff.

Semidiurnal tides with a mean tidal range of 1.1 m result in well-mixed water in two environmentally distinct zones of the slough (Broenkow 1977). The area above the mean tidal prism, which is about 4.8 km inland, has a water residence time in excess of 300 d. Salinity in this region of the slough varied seasonally with evaporation, precipitation, and runoff, and ranged from 17‰ in March to 37‰ in June. Water temperature ranged from 12°C to 26°C. Water west of the tidal prism (about 75% of the mean high water volume) is exchanged daily and reflects nearshore ocean conditions, with cooler temperatures (12–18°C) and more constant salinity (29–34‰).

Our study also included Bennett Slough, a shallow (0.3–1.8 m) semi-enclosed embayment that is connected to Elkhorn Slough via a culvert (0.6 m diameter) at the north end of Moss Landing Harbor (Fig. 1). Substratum was soft mud, mean water temperature ranged from 10.5°C in January to 21.5°C in June, and mean salinity was constant, varying from 30‰ in February to 33‰ in June (Appiah 1977).

### SAMPLING METHODS

Fishes were collected at least monthly from August 1974 to June 1976 at three locations in the main channel of Elkhorn Slough, approximately 0.6 km (the bridge station), 3.1 km (the dairy station), and 6.0 km (the Kirby Park station) inland, and at two locations on the sandy shelf (water depth = 5–10 m) north and south of the Moss Landing Harbor entrance (the ocean station; Fig. 1). At least

monthly collections were taken in the main channel at the Hudson's Landing station (about 10 km inland from the entrance of the slough) from January 1979 to June 1980 and in two tidal creeks (the Long Canyon and Rubis Creek stations) from October 1978 to June 1980. Fishes were collected about monthly in Bennett Slough from August 1974 to August 1976.

Collections in the main channel were taken with a 4.8 m otter trawl (3.8 cm stretch-mesh body with 1.3 cm codend liner) towed at 3–4 knots behind a 5 m Boston Whaler for 5 min or 10 min into the current at flood tide. In tidal creeks, this gear was towed at 1.5–2.5 knots between fixed markers during daylight. Catch data from otter trawls were standardized to number of fish per 10-min tow for seasonal and spatial comparisons. Plots of cumulative number of species against a randomly pooled number of samples (collected at the dairy station from May to October, 1975 and 1976, a period of high species richness) indicated that six tows were adequate to describe spatial and temporal patterns in species composition and abundance in the slough environment (Cailliet et al. 1977).

Collections in Bennett Slough were taken with a beach seine (15.2 m long with 0.6 cm and 1.3 cm meshes) fished along shore for an average of 30 m per haul to a maximum depth of 1.3 m. In areas of the tidal creeks that were <1.5 m in depth, fishes were collected periodically with beach seines and channel nets made of 3–6 mm<sup>2</sup> mesh nylon, similar to those of Bozeman and Dean (1980). At high-high slack tide, 8–10 channel nets were placed across creeks and tributaries, lead line forced into the sediment and ends secured above the channel bank. Fishes were collected as tidal level dropped and nets were exposed. Catch data from beach seines and channel nets were expressed as number of fish per haul.

Fishes were identified, counted, measured to the nearest mm in standard length (SL), and either released or preserved with 10% formalin.

Abundance (mean number of fishes per species per tow), species richness (mean number of species per tow), and dominance ( $D = \sum P_i^2$ , where  $P_i$  is the proportional abundance of species  $i$  per tow) were evaluated by location for each season. The index of dominance measures unevenness of species abundance within an assemblage, gives relatively little weight to rare species, and ranges from  $1 \times s^{-1}$  (where  $s$  = total number of species) to 1 (total dominance by one species). Seasons were defined as fall (August, September, October), winter (November, December, January), spring (February, March, April), and summer (May, June, July). These groupings approximated the climatic seasonality of the study area in terms of rainfall, air

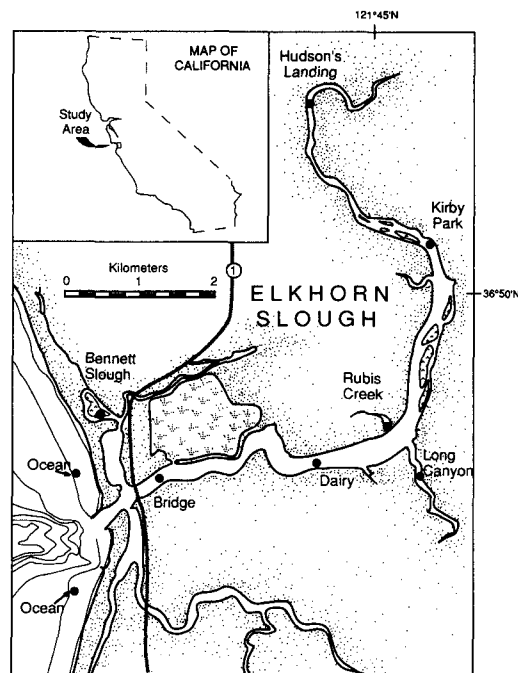


Fig. 1. Fish sampling locations (●) in Elkhorn and Bennett sloughs, California, and the adjacent nearshore ocean.

and water temperatures, and salinity (Broenkow 1977).

Species composition was compared between stations using the percentage similarity index (PSI; Krebs 1989):

$$PSI = \sum \text{minimum}(p_{1i}, p_{2i})$$

where PSI is the sum of the smallest percentage by number ( $p_{1i}$  and  $p_{2i}$ ) of each pair of species  $i$  from stations 1 and 2, respectively. This index ranges from zero (no similarity) to 1.00 (identical species arrays). In the present study, PSI values greater than 0.60 were interpreted as significant, based on level of significance of product-moment correlation coefficient relative to PSI's (Cailliet and Barry 1978).

Each species was categorized (modified from Lenanton and Potter 1987; Loneragan et al. 1989) as either (1) a slough resident (R; spawns and completes entire life cycle in the slough); (2) a partial resident (PR; primarily lives in the slough, seasonally or ontogenetically moves to the ocean, and returns to reproduce in the slough); (3) marine immigrant (MI; primarily lives in the ocean and

TABLE 1. Relative abundance (%), mean number per 10-min tow (n), standard error (in parentheses), and life style (M = marine, MI = marine immigrant, R = slough resident, PR = partial resident, and F = freshwater) of fish species caught in otter trawls at six locations in Elkhorn Slough and at two nearshore ocean stations. Only those species representing >0.1% overall abundance are included. Overall abundance and rank are indicated. Dash (—) indicates species was not collected.

Taxon	Ocean		Bridge		Dairy	
	n	%	n	%	n	%
<i>Amphistichus argenteus</i> (M)	0.57 (0.27)	4.6	—	—	—	—
<i>Atherinops affinis</i> (PR)	—	—	1.14 (1.14)	0.5	0.02 (0.02)	<0.1
<i>Atherinopsis californiensis</i> (PR)	—	—	0.03 (0.03)	<0.1	0.06 (0.05)	0.1
<i>Citharichthys stigmaeus</i> (MI)	2.74 (0.55)	21.9	21.54 (6.66)	10.3	2.92 (0.92)	4.4
<i>Clevelandia ios</i> (R)	—	—	0.03 (0.03)	<0.1	—	—
<i>Clupea pallasii</i> (MI)	—	—	—	—	1.67 (1.61)	2.5
<i>Cymatogaster aggregata</i> (PR)	0.46 (0.32)	3.7	90.94 (69.10)	43.4	19.06 (4.69)	28.8
<i>Damalichthys vacca</i> (MI)	0.08 (0.06)	0.6	1.77 (0.55)	0.8	1.27 (0.35)	1.9
<i>Dorosoma petenense</i> (F)	—	—	—	—	—	—
<i>Embiotoca jacksoni</i> (R)	0.01 (0.01)	0.1	30.49 (7.02)	14.6	8.88 (2.73)	13.4
<i>Engraulis mordax</i> (MI)	—	—	0.66 (0.66)	0.3	0.10 (0.07)	0.2
Gobiidae	—	—	—	—	—	—
<i>Hyperprosopon anale</i> (M)	1.76 (0.57)	14.1	—	—	—	—
<i>Hyperprosopon argenteum</i> (MI)	0.07 (0.04)	0.6	1.63 (0.77)	0.8	0.86 (0.32)	1.3
<i>Hypsopsetta guttulata</i> (MI)	0.04 (0.02)	0.3	—	—	0.08 (0.05)	0.1
<i>Lepidogobius lepidus</i> (R)	—	—	0.17 (0.12)	0.1	0.06 (0.05)	0.1
<i>Leptocottus armatus</i> (R)	0.03 (0.03)	0.2	2.06 (0.96)	1.0	1.57 (0.50)	2.4
<i>Micrometrus minimus</i> (M)	0.01 (0.01)	0.1	1.17 (0.40)	0.6	0.37 (0.29)	0.6
<i>Morone saxatilis</i> (F)	—	—	—	—	—	—
<i>Mustelus californicus</i> (M)	—	—	—	—	—	—
<i>Myliobatis californica</i> (PR)	0.01 (0.01)	0.1	0.14 (0.06)	0.1	0.14 (0.05)	0.2
<i>Neoclinus uninotatus</i> (M)	—	—	0.40 (0.29)	0.2	—	—
<i>Ophiodon elongatus</i> (M)	0.22 (0.10)	1.8	0.34 (0.15)	0.2	0.02 (0.02)	<0.1
<i>Paralichthys californicus</i> (MI)	0.01 (0.01)	0.1	0.03 (0.03)	<0.1	—	—
<i>Parophrys vetulus</i> (MI)	0.53 (0.14)	4.2	7.14 (2.61)	3.4	2.63 (0.88)	4.0
<i>Phanerodon furcatus</i> (PR)	0.58 (0.20)	4.6	34.80 (8.17)	16.6	18.78 (4.63)	28.4
<i>Platichthys stellatus</i> (MI)	0.64 (0.13)	5.1	9.36 (1.09)	4.5	2.59 (0.41)	3.9
<i>Pleuronichthys decurrens</i> (M)	1.08 (0.68)	8.6	0.23 (0.12)	0.1	0.06 (0.03)	0.1
<i>Porichthys notatus</i> (MI)	—	—	0.29 (0.23)	0.1	0.61 (0.35)	0.9
<i>Psettichthys melanostictus</i> (M)	2.37 (0.55)	19.0	—	—	—	—

TABLE 1. Continued.

Kirby Park		Hudson's Landing		Long Canyon		Rubis Creek		Overall		Rank
n	%	n	%	n	%	n	%	n	%	
—	—	—	—	—	—	—	—	0.12	0.2	24
0.20	0.3	0.42	0.4	0.56	4.9	0.03	0.1	0.28	0.4	20
(0.13)		(0.36)		(0.21)		(0.03)				
0.16	0.2	—	—	—	—	0.06	0.2	0.04	0.1	31
(0.09)						(0.04)				
0.04	0.1	0.03	<0.1	0.03	0.3	0.10	0.3	3.14	5.0	6
(0.03)		(0.19)		(0.03)		(0.09)				
—	—	0.33	0.3	0.43	3.7	0.68	1.8	0.20	0.3	22
		(0.14)		(0.35)		(0.10)				
0.80	1.0	15.23	15.0	0.19	1.7	1.47	3.8	2.46	3.9	8
(0.34)		(6.21)		(0.11)		(0.89)				
41.71	53.7	1.58	1.6	0.34	3.0	5.98	15.5	18.54	29.4	1
(8.94)		(0.46)		(0.16)		(2.49)				
0.31	0.4	—	—	—	—	0.32	0.8	0.46	0.7	11
(0.10)						(0.14)				
0.59	0.8	0.40	0.4	—	—	0.03	0.1	0.14	0.2	24
(0.57)		(0.23)				(0.03)				
2.16	2.8	—	—	0.43	3.7	2.97	7.7	5.01	8.0	4
(0.99)				(0.16)		(0.65)				
3.61	4.6	18.65	18.3	0.22	1.9	3.55	9.2	3.42	5.4	5
(2.06)		(6.45)		(0.16)		(2.03)				
—	—	0.08	0.1	0.19	1.7	0.10	0.3	0.05	0.1	31
		(0.06)		(0.16)		(0.05)				
—	—	—	—	—	—	—	—	0.38	0.6	13
0.27	0.3	0.03	<0.1	—	—	0.13	0.3	0.35	0.6	13
(0.15)		(0.19)				(0.08)				
0.06	0.1	0.03	<0.1	0.06	0.5	0.03	0.1	0.05	0.1	31
(0.03)		(0.19)		(0.06)		(0.03)				
0.47	0.6	—	—	0.03	0.3	—	—	0.09	0.1	31
(0.37)				(0.03)						
10.20	13.1	58.67	57.6	5.89	51.2	15.87	41.1	12.20	19.4	2
(5.48)		(14.28)		(1.79)		(5.24)				
—	—	—	—	—	—	0.16	0.4	0.19	0.3	22
						(0.14)				
—	—	0.66	0.6	—	—	—	—	0.08	0.1	31
		(0.30)								
0.02	<0.1	0.31	0.3	—	—	0.03	0.1	0.05	0.1	31
(0.02)		(0.18)				(0.03)				
0.76	1.0	0.53	0.5	0.25	2.2	0.74	1.9	0.35	0.6	13
(0.25)		(0.35)		(0.14)		(0.44)				
—	—	—	—	—	—	—	—	0.04	0.1	31
—	—	—	—	—	—	0.03	0.1	0.09	0.1	31
						(0.03)				
0.02	<0.1	0.82	0.8	0.19	1.7	1.14	3.0	0.30	0.5	18
(0.02)		(0.21)		(0.07)		(0.36)				
8.33	10.7	0.75	0.7	—	—	0.74	1.9	2.53	4.0	7
(4.81)		(0.30)				(0.44)				
1.73	2.2	—	—	0.19	1.7	0.52	1.3	6.49	10.3	3
(0.34)				(0.08)		(0.20)				
4.57	5.9	2.10	2.1	0.68	5.9	0.43	1.1	2.47	3.9	8
(0.95)		(0.79)		(0.18)		(0.15)				
—	—	—	—	—	—	—	—	0.26	0.4	20
0.88	1.1	0.26	0.3	—	—	0.13	0.3	0.29	0.5	18
(0.74)		(0.12)				(0.08)				
—	—	—	—	—	—	—	—	0.51	0.8	10

TABLE 1. Continued.

Taxon	Ocean		Bridge		Dairy	
	n	%	n	%	n	%
<i>Rhacochilus toxotes</i> (M)	0.01 (0.01)	0.1	0.80 (0.48)	0.4	0.10 (0.04)	0.2
<i>Scorpaenichthys marmoratus</i> (MI)	0.07 (0.03)	0.6	3.71 (1.50)	1.8	0.55 (0.20)	0.8
<i>Sebastes</i> spp.	0.05 (0.03)	0.4	0.34 (0.23)	0.2	0.20 (0.15)	0.3
<i>Sebastes auriculatus</i> (M)	—	—	1.26 (0.59)	0.6	1.67 (0.76)	2.5
<i>Sebastes mystinus</i> (M)	0.07 (0.04)	0.6	0.60 (0.20)	0.3	0.53 (0.22)	0.8
<i>Sebastes paucispinis</i> (M)	0.08 (0.06)	0.6	0.20 (1.02)	0.1	0.41 (0.29)	0.6
<i>Seriphus politus</i> (MI)	—	—	—	—	—	—
<i>Spirinchus starksi</i> (M)	0.45 (0.38)	3.6	0.03 (0.03)	<0.1	—	—
<i>Symphurus atricauda</i> (MI)	—	—	0.09 (0.06)	<0.1	—	—
<i>Syngnathus leptorhynchus</i> (R)	0.09 (0.04)	0.7	0.17 (0.10)	0.1	0.04 (0.03)	0.1
<i>Triakis semifasciata</i> (PR)	—	—	0.06 (0.06)	<0.1	0.16 (0.11)	0.2
<i>Urolophus halleri</i> (M)	—	—	—	—	0.16 (0.08)	0.2

regularly enters the slough at some stage of life to feed, reproduce, or use the area as a nursery); (4) marine (M; coastal species rarely or never found in Elkhorn Slough); or (5) freshwater (F; primarily lives and reproduces in freshwater, but found rarely in the most inland area of the slough). Members of the resident and partial resident categories potentially can spawn and complete their life cycle outside the slough environment. Studies on the ichthyoplankton of Elkhorn Slough (Wang 1981; Yoklavich et al. 1992) and life histories of fishes in West Coast estuaries (NOAA 1990) were used to classify some species. The relative contribution made by number of individuals and number of species in each category to the fish assemblage of each slough region was evaluated. Regions were defined as upper slough and tidal creeks (Hudson's Landing, Long Canyon, and Rubis Creek stations), middle slough (Kirby Park station), lower slough (dairy and bridge stations), and Bennett Slough.

### Results

A total of 22,334 fishes, representing 65 species from 27 families, was collected in 355 otter trawl tows at six stations in the main channel and tidal creeks of Elkhorn Slough and two nearshore ocean stations during 44 months between August 1974 and June 1980 (Table 1). Ten species accounted for >90% of all fishes taken in trawls throughout the study; relative abundance of these species ranged from 0.8% for *Psettichthys melanostictus*

(sandsole), occurring only at the ocean station, to 29.4% for *Cymatogaster aggregata* (shiner surfperch), which was abundant at all stations.

The highest abundance and species richness occurred at the bridge station, where a mean density of 209 fish per 10-min tow and 37 species were collected in 35 tows (Table 2). The relatively high standard error (SE = 82.4) is largely due to 1,208 *C. aggregata* from a single collection during an intense episode of red tide. The large number of individuals and species likely reflects increased diversity of available habitat at the bridge station, including submerged rocks and pier pilings. Species more typical of rocky coastal marine habitats were collected in low numbers at the bridge station, including *Artedius harringtoni* (scalyhead sculpin), *Coryphopterus nicholsii* (blackeye goby), *Hexagrammos decagrammos* (kelp greenling), *Hypsurus caryi* (rainbow surfperch), *Neoclinus uninotatus* (onespot fringehead), *Ophiodon elongatus* (lingcod), *Scorpaenichthys marmoratus* (cabezon), and juvenile *Sebastes*, especially *S. auriculatus* (brown rockfish), *S. mystinus* (blue rockfish), *S. paucispinis* (bocaccio), and *S. rastrelliger* (grass rockfish; see Cailliet et al. [1977] for the abundance of less common species).

The ocean station and tidal creeks (Long Canyon and Rubis Creek stations) consistently had the lowest mean densities (12.5, 11.5, and 38.7 fish per 10-min tow, respectively, Table 2). The other three stations (i.e., dairy, Kirby Park, and Hudson's Landing) along the main channel were interme-

TABLE 1. Continued.

Kirby Park		Hudson's Landing		Long Canyon		Rubis Creek		Overall		Rank
n	%	n	%	n	%	n	%	n	%	
—	—	—	—	—	—	—	—	0.10	0.2	24
0.10 (0.05)	0.1	—	—	—	—	—	—	0.47	0.7	11
—	—	—	—	—	—	0.06 (0.09)	0.2	0.08	0.1	31
0.04 (0.04)	0.1	—	—	—	—	0.23 (0.12)	0.6	0.39	0.6	13
—	—	—	—	—	—	—	—	0.15	0.2	24
—	—	—	—	—	—	—	—	0.09	0.1	31
0.20 (0.13)	0.3	0.03 (0.19)	<0.1	1.09 (1.08)	9.5	0.09 (0.05)	0.2	0.06	0.1	31
—	—	—	—	—	—	—	—	0.10	0.2	24
—	—	0.22 (0.15)	0.2	0.12 (0.10)	1.0	0.60 (0.26)	1.6	0.14	0.2	24
—	—	—	—	—	—	0.58 (0.20)	1.5	0.12	0.2	24
0.27 (0.11)	0.3	0.29 (0.18)	0.3	0.43 (0.22)	3.7	1.55 (0.38)	4.0	0.36	0.6	13
0.14 (0.09)	0.2	—	—	—	—	—	—	0.04	0.1	31

diate in fish abundance. Species richness was highest at the three stations closest to the entrance of the slough (i.e., ocean, bridge, and dairy) and at the Rubis Creek station; overall dominance indices were lowest at these stations (Table 2).

Species composition of otter trawl catches was most similar between the bridge station and the other two stations in the main channel of the lower and middle region of Elkhorn Slough (i.e., dairy and Kirby Park, Table 3), largely because of the numerically dominant *C. aggregata* and other surfperch species. Fish assemblages at the most shallow inland station of the main channel (Hudson's Landing) and at the tidal creek stations (Rubis Creek and Long Canyon) were more similar to each other than to assemblages at any other station in the main channel. Species composition was most unique at the ocean station and similarity (PSI) to the other

stations decreased progressively with distance inland and into the tidal creeks.

Dominant species at each site varied with distance inland (Table 4). Of the eight most abundant species taken at the ocean station, four were nonestuarine species not collected at any slough station, and representing nearly 50% of the total abundance at this station. Two abundant species were restricted to the ocean, bridge, and dairy stations. Notably, *Citharichthys stigmaeus* (speckled sanddab), the dominant species at the ocean station, and *Phanerodon furcatus* (white surfperch) were much less abundant east of the dairy station. *Cymatogaster aggregata* was numerically dominant at lower and middle slough stations of the main channel and in Rubis Creek. *Leptocottus armatus* (staghorn sculpin), a euryhaline cottid, was highest in abundance at stations furthest inland, and was the dominant spe-

TABLE 2. Summary of diversity, dominance, and abundance of fishes captured with otter trawls at six stations in Elkhorn Slough and at two nearshore ocean stations.

	Ocean	Bridge	Dairy	Kirby Park	Hudson's Landing	Long Canyon	Rubis Creek	Overall
Number of species	34	37	37	26	24	20	32	65
Dominance index	0.12	0.26	0.19	0.32	0.37	0.29	0.22	
Total number*	950	7,326	3,244	3,807	4,479	596	1,933	22,334
Mean number tow <sup>-1</sup>	12.5	209.3	66.2	77.7	101.8	11.5	38.7	63.0
(SE)	(1.6)	(82.4)	(2.0)	(15.3)	(21.8)	(1.7)	(9.6)	
Number of tows	76	35	49	49	44	52	50	355

\* Adjusted to 10-min tows.

TABLE 3. Comparison of fish species composition in otter trawl collections from six stations in Elkhorn Slough and two adjacent ocean stations based on percentage similarity index (PSI). Comparisons with the fish assemblage from beach seine collections in Bennett Slough also are indicated.

	Bridge	Dairy	Kirby Park	Hudson's Landing	Rubis Creek	Long Canyon	Bennett Slough
Ocean	0.30	0.25	0.17	0.05	0.11	0.11	0.08
Bridge	—	0.77	0.60	0.07	0.32	0.16	0.12
Dairy	—	—	0.48	0.11	0.36	0.18	0.14
Kirby Park	—	—	—	0.27	0.45	0.32	0.28
Hudson's Landing	—	—	—	—	0.61	0.62	0.30
Rubis Creek	—	—	—	—	—	0.66	0.35
Long Canyon	—	—	—	—	—	—	0.42

cies in trawls at the Hudson's Landing and tidal creek stations. *Engraulis mordax* (northern anchovy) and *Clupea pallasii* (Pacific herring) also were numerically dominant in otter trawls at the shallow inland stations.

For beach seine and channel net collections from the smallest tidal creeks (Table 5), overall species richness was only 16 (<10 species in the shallowest creeks) and dominance was higher (0.45–0.60) than in the main channel. Dominance indices increased because of the high relative abundance of juvenile *Atherinops affinis* (topsmelt, 62.7%). *Clevelandia ios* (arrow goby) and *E. mordax* also were relatively abundant (12.1% and 11.6%, respectively) in beach seine and channel net collections from the upper marshes.

Seasonal variation in fish abundance was high, with a noticeable depression in mean catch rate during the winter and early spring at most stations (Fig. 2). The exceptionally high peak in abundance at the bridge station during winter 1978 was caused

by one large catch of *C. aggregata*. Peak abundance occurred in summer at most stations throughout the slough. Mean species richness per tow also decreased during winter (Fig. 3). Species collected in winter largely were slough residents (see Cailliet et al. [1977] and Barry [1983] for monthly species-specific catch rates). Seasonal patterns in mean dominance indices generally were opposite those in abundance and species richness, with peaks in winter and early spring months (Fig. 3). Trends in dominance were most apparent at the ocean station and lower slough stations (i.e., bridge and dairy) in the main channel.

During spring and summer, most species were present as juveniles, while some were collected in low numbers as reproductively active adults, including *C. pallasii*, *C. aggregata*, *Embiotoca jacksoni* (black surfperch), *Triakis semifasciata* (leopard shark), and *Myliobatis californica* (bat ray). Juvenile fishes contributed to the increase in abundance and species richness during this period, and many of

TABLE 4. Relative abundance (%) of dominant species totaling 80% (or greater) of the fishes collected in Elkhorn and Bennett sloughs and at adjacent nearshore ocean stations. See legend of Table 1 for coded life-style categories (in parentheses).

Species	Ocean	Bridge	Dairy	Kirby Park	Hudson's Landing	Long Canyon	Rubis Creek	Bennett Slough
<i>Psettichthys melanostictus</i> (M)	19.0							
<i>Hyperprosopon anale</i> (M)	14.1							
<i>Pleuronichthys decurrens</i> (M)	8.6							
<i>Amphistichus argenteus</i> (M)	4.6							
<i>Citharichthys stigmaeus</i> (MI)	21.9	10.3	4.4					
<i>Phanerodon furcatus</i> (PR)	4.6	16.6	28.4					
<i>Parophrys vetulus</i> (MI)	4.2		4.0	10.7				
<i>Platichthys stellatus</i> (MI)	5.1		3.9	5.9		5.9		22.0
<i>Cymatogaster aggregata</i> (PR)		43.4	28.8	53.7			15.5	
<i>Embiotoca jacksoni</i> (R)		14.6	13.4			3.7	7.7	
<i>Leptocottus armatus</i> (R)				13.1	57.6	51.2	41.1	23.7
<i>Engraulis mordax</i> (MI)					18.3		9.2	
<i>Clupea pallasii</i> (MI)					15.0		3.8	
<i>Seriophilus politus</i> (MI)						9.5		
<i>Atherinops affinis</i> (PR)						4.9		
<i>Clevelandia ios</i> (R)						3.7		34.9
<i>Triakis semifasciata</i> (PR)						3.7	4.0	
Total (%)	82.1	84.9	82.9	83.4	90.9	82.6	81.3	80.6
Number of dominant species	8	4	6	4	3	7	6	3



TABLE 5. Number (Number = mean per sample and Percent = relative abundance) of fishes caught in beach seines in Bennett Slough from August 1974 to August 1976, and in beach seines and channel nets at the most shallow stations of Elkhorn Slough (i.e., Long Canyon, Rubis Creek, and Hudson's Landing) from October 1978 to June 1980. See legend of Table 1 for coded life-style categories (in parentheses).

Taxon	Bennett Slough		Elkhorn Slough	
	Number	Percent	Number	Percent
<i>Acanthogobius flavimanus</i> (R)	0.3	0.4	0.7	1.1
<i>Atherinops affinis</i> (PR)	1.5	2.6	38.9	62.7
<i>Atherinopsis californiensis</i> (PR)	0.6	1.1	—	—
<i>Clevelandia ios</i> (R)	20.6	34.9	7.5	12.1
<i>Clupea pallasii</i> (MI)	0.6	1.0	—	—
<i>Cottus asper</i> (F)	<0.1	<0.1	—	—
<i>Cymatogaster aggregata</i> (PR)	1.0	1.7	<0.1	0.1
<i>Embiotoca jacksoni</i> (R)	1.7	2.8	0.2	0.3
<i>Engraulis mordax</i> (MI)	0.2	0.4	7.2	11.6
<i>Eucyclogobius newberryi</i> (R)	0.1	0.1	—	—
<i>Gasterosteus aculeatus</i> (F)	0.9	1.5	0.2	0.3
<i>Gillichthys mirabilis</i> (R)	—	—	2.4	3.9
Gobiidae	—	—	1.9	3.1
<i>Hyperprosopon argenteum</i> (MI)	<0.1	<0.1	—	—
<i>Hypomesus pretiosus</i> (M)	1.3	2.3	—	—
<i>Hypsopsetta guttulata</i> (MI)	—	—	<0.1	<0.1
<i>Lepidogobius lepidus</i> (R)	1.0	1.7	—	—
<i>Leptocottus armatus</i> (R)	14.0	23.7	2.2	3.5
<i>Mugil cephalus</i> (R)	—	—	0.1	0.1
<i>Paralichthys californicus</i> (MI)	—	—	0.1	0.1
<i>Phanerodon furcatus</i> (PR)	0.2	0.3	—	—
<i>Platichthys stellatus</i> (MI)	13.0	22.0	<0.1	<0.1
<i>Porichthys notatus</i> (MI)	1.1	1.8	0.7	1.1
<i>Syngnathus leptorhynchus</i> (R)	1.0	1.8	—	—
<i>Triakis semifasciata</i> (PR)	—	—	0.1	0.1
<i>Urolophus halleri</i> (M)	<0.1	0.1	—	—
Mean number of fish sample <sup>-1</sup>	59.1		62.1	
Total number of fish	5,074		3,352	
Number of species	20		16	
Number of samples	86		54	

these species no longer were in the slough by the following fall. These fishes may enter the slough in summer or become available to collection gear after being spawned in the slough during spring and summer. For example, the abundance and distribution of *Parophrys vetulus* (English sole) were distinctly seasonal, with a steady increase in abundance of juveniles at all stations in the main channel during spring, and a peak at the Kirby Park station in summer (mean length = 76 mm SL). *Parophrys vetulus* was not taken from the Kirby Park station during fall months, but increased in abundance at the ocean station during that period (mean SL = 134 mm).

A total of 5,074 fishes was collected by beach seine (n = 86 samples) in Bennett Slough from August 1974 to August 1976 (Table 5). Although the total number of species (20) was relatively low, average density (59.1 fish per sample) was high. Three euryhaline species, *C. ios*, *L. armatus*, and *Platichthys stellatus* (starry flounder), were most abundant and accounted for 80.6% of the total catch (Table 4). *Leptocottus armatus* and *P. stellatus*

were collected from Bennett Slough in all months of the year; *C. ios* were not collected during winter.

*Clevelandia ios* was the most numerous species in Bennett Slough, contributing 34.9% of the total catch and numerically dominating (59%) the catch in summer months. This gobiid also ranked second in beach seine and channel net collections from the tidal creeks and the Hudson's Landing station in upper Elkhorn Slough (Table 5). In contrast, *C. ios* ranked 22 of 42 species and contributed only 0.3% to the overall catch from otter trawls taken throughout Elkhorn Slough. This species was essentially absent from the ocean, lower, and middle slough otter trawl collections and was collected only in low numbers in trawls at the tidal creeks and Hudson's Landing stations (Table 1).

Like *C. ios*, *L. armatus* was most abundant in Bennett Slough during summer months (32% of the catch); those collected in summer were immature and <120 mm SL. During spring, maximum mean length of *L. armatus* was 149 mm SL, which is larger than the size at first maturity (120 mm TL; Jones 1962). *Platichthys stellatus* dominated (60%) the catch

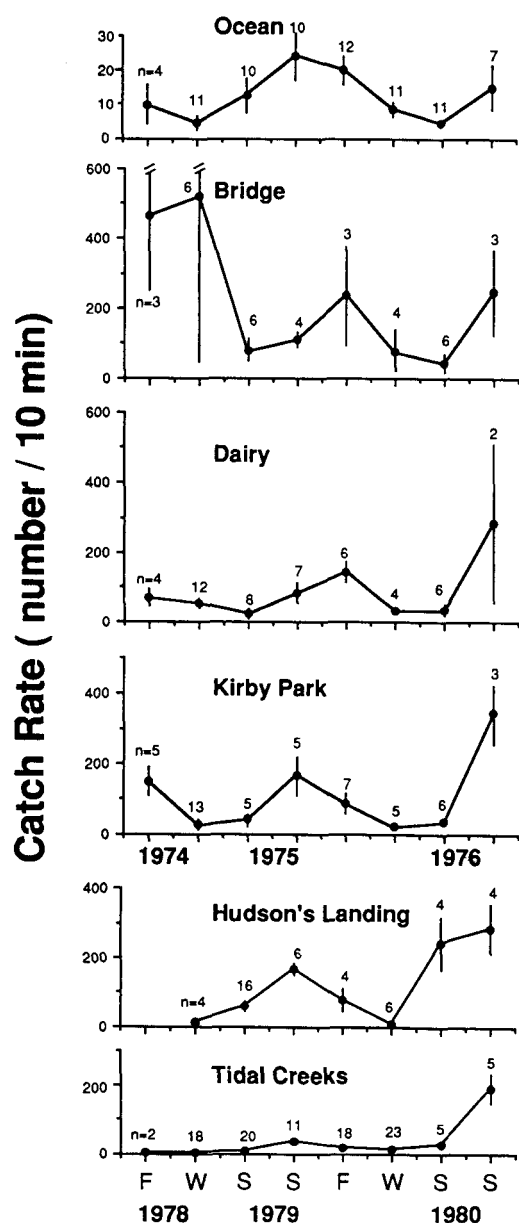


Fig. 2. Seasonal variation in mean catch (number per 10-min tow) of fish from otter trawls at each location in Elkhorn Slough, California; data from Long Canyon and Rubis Creek were combined into one tidal creek location. Vertical bars indicate standard errors. Number of samples (n) is indicated above data points.

during winter, and its mean standard length ranged from 33 mm in June to 258 mm in March. Because length at maturity is about 300 mm SL for males and 350 mm SL for females (Orcutt 1950), all *P. stellatus* taken in Bennett Slough were immature.

Although catch rates from seine collections in Bennett Slough are not comparable directly to those from otter trawls in Elkhorn Slough, relative abundance and species composition can be evaluated between the two sloughs. The majority of the fishes found in Bennett Slough also were common in Elkhorn Slough, even though indices of similarity between the two sites were low (Table 3). Species similarity increased with distance inland, and was greatest between the Bennett Slough assemblage and those at the tidal creek and Hudson's Landing stations, primarily because of the numerical dominance of *L. armatus* and *P. stellatus*. Dominance indices were highest for fish assemblages at the Bennett Slough and Hudson's Landing stations; only three species represented >80% of the total fish abundance at these stations (Table 4). Species assemblages were least similar between Bennett Slough and the ocean station.

Notably, *Acanthogobius flavimanus* (yellowfin goby), a euryhaline species introduced from Japan (Brittan et al. 1970), and *Gasterosteus aculeatus* (three-spine stickleback), primarily a freshwater species, were only collected by beach seines in Bennett Slough and the most shallow areas of Elkhorn Slough (Table 5). *Cottus asper* (prickly sculpin), also a freshwater species, *Eucyclogobius newberryi* (tide-water goby), and juvenile (<50 mm SL) *Hypomesus pretiosus* (surf smelt), a marine species only found as larvae in Elkhorn Slough (Yoklavich et al. 1992), were collected only in Bennett Slough regardless of sampling gear. As in Elkhorn Slough, species richness in Bennett Slough was low in winter and early spring (mean of six species per haul) and high in summer and early fall (a mean of 10–11 species per haul).

The ichthyofauna in otter trawl collections from Elkhorn Slough included a large number of marine species (Table 6), ranging from 55% to 66% of upper and lower slough species, respectively. About half of the marine species in the lower slough were marine immigrants (or slough opportunists) and the rest were uncommon species from nearshore habitats. Over 70% of the marine species in the upper slough were marine immigrants, using the slough as spawning and nursery grounds. Marine immigrants contributed from 21.5% to 32.3% of the total number of fishes collected throughout the slough. The relative abundance of strictly marine fishes declined from 2.7% in the lower slough to 0.6% in the upper slough.

Resident and partial-resident species occurred

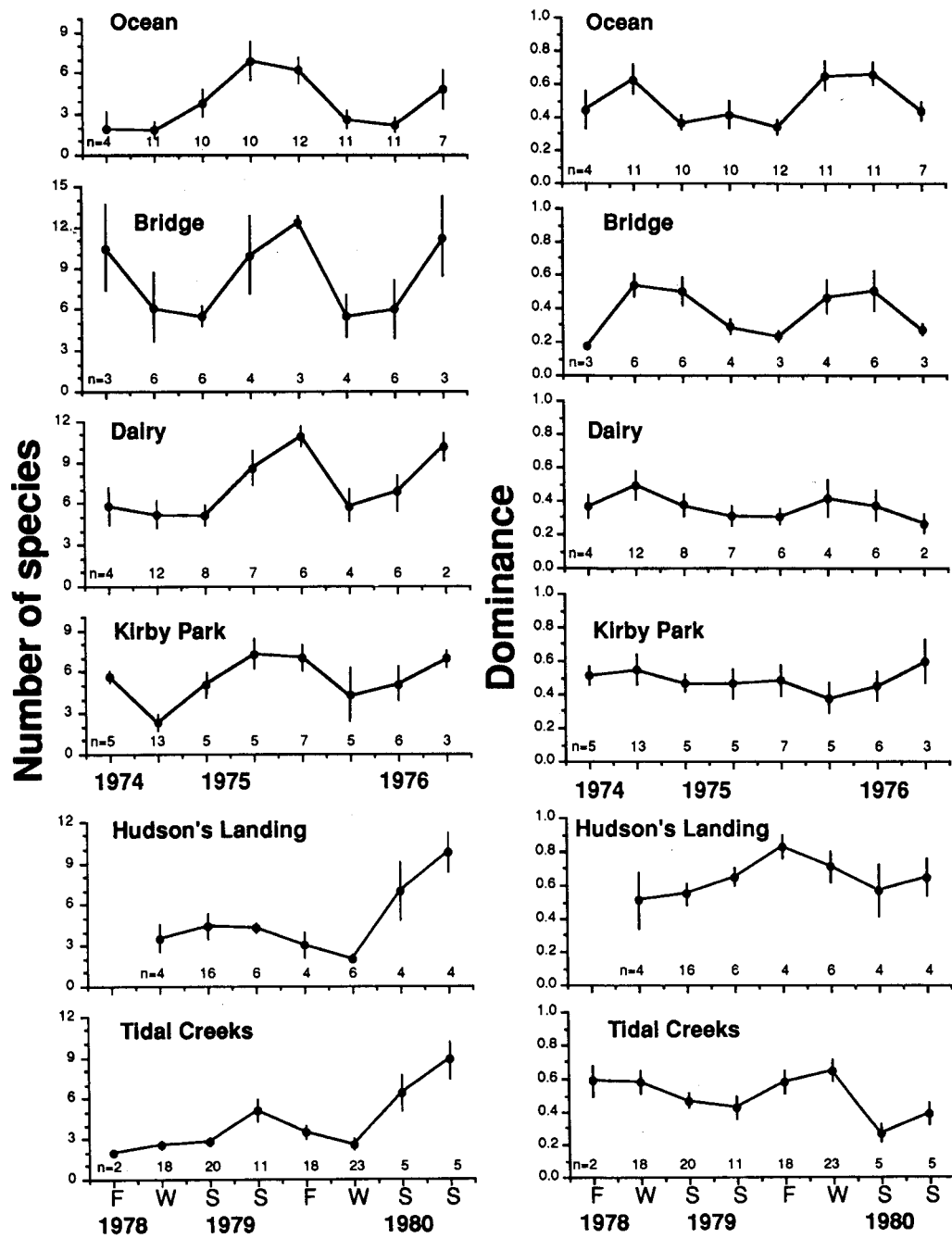


Fig. 3. Seasonal variation in diversity (mean number of species and mean dominance index per 10-min tow) of fish from otter trawls at each location in Elkhorn Slough, California; data from Long Canyon and Rubis Creek were combined into one tidal creek location. Vertical bars indicate standard errors. Number of samples (n) is indicated above data points.

TABLE 6. Number and percentage of species and individuals contributing to each life-style category from otter trawl collections of fishes taken in the lower (bridge and dairy stations), middle (Kirby Park station), and upper (Hudson's Landing and tidal creek stations) regions of Elkhorn Slough and from beach seine collections of fishes taken in Bennett Slough. Only species >0.1% of total abundance were evaluated.

Life-style Category	Elkhorn Slough							
	Lower		Middle		Upper		Bennett Slough	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Species								
Marine	10	30.3	3	12.0	5	16.1	2	10.0
Marine immigrant	12	36.4	12	48.0	12	38.7	5	25.0
Slough resident	5	15.2	3	12.0	6	19.4	7	35.0
Partial resident	6	18.2	6	24.0	6	19.4	4	20.0
Freshwater	—	—	1	4.0	2	6.5	2	10.0
Total	33		25		31		20	
Individuals								
Marine	285	2.7	27	0.7	41	0.6	122	2.4
Marine immigrant	2,273	21.5	925	24.3	2,264	32.3	1,279	25.2
Slough resident	1,681	15.9	628	16.5	3,972	56.7	3,308	65.2
Partial resident	6,331	59.9	2,197	57.7	666	9.5	289	5.7
Freshwater	—	—	30	0.8	47	0.7	76	1.5
Total	10,570		3,807		6,990		5,074	

throughout the slough in equal proportions. The proportion of the total number of resident fishes increased from 15.9% in the lower slough to 56.7% in the upper slough. Numbers of fishes with partial-resident status were exceptionally high (58–60%) in the lower and middle regions, largely due to *C. aggregata* (this species is found in all but some winter months). Freshwater species were found only in the middle and upper slough regions.

Over 70% of the total number of fishes collected in Bennett Slough, represented by 11 species (55% of the total number of species), were categorized as resident and partial-resident slough species (Table 6). The relative number of resident species (35%) and proportion of total individuals (65.2%) was higher here than at any location in Elkhorn Slough. Marine and freshwater species each comprised only 10% of all species, representing 2.4% of the total catch. The proportion of marine immigrant individuals was comparable to that in Elkhorn Slough, but this category included fewer species in Bennett Slough.

### Discussion

The ichthyofauna of Elkhorn Slough is characterized by a few dominant species that reside year-round within the system or leave only for brief periods, and several seasonally dominant species that enter the slough as reproductively active adults or as juveniles. Seasonal and spatial variations in abundance, species richness, and distribution of fish assemblages in Elkhorn Slough and adjacent habitats are similar to patterns described for other estuarine systems. Higher abundance and species

richness during the summer invasion of young-of-the-year marine species into the slough also have been documented for fish assemblages in other temperate bays and estuaries, and were positively correlated with temperature (Allen and Horn 1975; Hoff and Ibara 1977; Allen 1982; Onuf and Quammen 1983). The decline in species richness and change in species composition with distance up Elkhorn Slough has been noted in other systems as well (Loneragan et al. 1986; Blaber et al. 1989). The lower slough is strongly influenced by marine hydrographic processes (Broenkow 1977), and therefore more accessible to coastal marine species. Dominant species of the upper slough and tidal creeks are best characterized as euryhaline, with affinities toward higher temperature. Higher temperature, nutrient content, and residence time of water above the tidal prism (approximately east of the dairy station; Smith 1973) enhance production of food for fishes in the upper slough and tidal creeks, but may exclude less thermally-tolerant marine species during some seasons.

Although species composition may vary latitudinally, the numerically dominant fishes in estuaries along the west coast of the United States are juvenile members of similar trophic levels (planktivores or low-level carnivores on infaunal invertebrates) and families (Atherinidae, Bothidae, Cottidae, Embiotocidae, Engraulidae, Gobiidae, Pleuronectidae). According to cluster analyses of Horn and Allen (1976), species composition of Elkhorn Slough fish assemblages is most similar to that of Morro Bay, and defines a unique faunal group for central California bays. More generally, fish assemblages of bays north of Point Conception were

distinguished from those of southern California (Horn and Allen 1976).

The maximum number of species found in any of these systems may be influenced by the surface area of the estuarine system (Horn and Allen 1976), as well as the structural complexity of the habitat (Weinstein and Brooks 1983; Weinstein 1985). The smaller tidal creeks and upper Elkhorn Slough stations supported fewer species than did the wide main channel with larger expanses of sand and mud bottom. Although Elkhorn Slough generally lacks the abundant submerged vegetation prevalent in other estuaries, the increased heterogeneity of habitat at the lower slough stations (due to submerged rocks and pilings, and commercial oyster racks) was accompanied by increased species richness. Recent restoration of temperate seagrass beds (*Zostera marina*) in Elkhorn Slough could increase species diversity, and modify the distribution and trophic structure of slough ichthyofauna to include more detritivores and epifaunal consumers (Whitfield 1988). Moreover, because survival during early life often delimits year-class success for marine fishes, increased availability of spawning substrate from eelgrass could enhance recruitment for those species with demersal adhesive eggs.

The characterization of fish assemblages in shallow bays often is confounded by the biases associated with collection techniques, which vary with season, location, and life stage of the fish (Weinstein and Davis 1980; Allen 1982; Horn and Allen 1985; Pierce et al. 1990). Avoidance of towed nets, such as otter trawls, by the largest, most active fishes (e.g., *Triakis semifasciata*, *Mustelus* spp. [smoothhounds], and *Morone saxatilis* [striped bass]), and by the adults of many schooling fishes (e.g., *Clupea pallasii*, *Engraulis mordax*, and the atherinids) contributes to the underestimation of abundance of these species, and likewise inflates the relative importance of gear-susceptible species. *Atherinops affinis* and *Atherinopsis californiensis* clearly were under represented in otter trawl collections, as indicated by the increased relative abundance in beach seine and channel net collections (Table 5) and in gill net collections (Ruagh 1976). Indeed, *A. affinis* contributed significantly to secondary production estimated from beach seine collections taken in a southern California estuary (Allen 1982). Extrusion of small adults (e.g., *E. mordax*) and juveniles from towed nets also results in an underestimate of their abundance. Otter trawls are inadequate to sample many members of Gobiidae, including the common residents *Clevelandia ios*, *Gillichthys mirabilis*, and *Acanthogobius flavimanus*. These species burrow in sand and mud substrate when disturbed, potentially avoiding the trawl, and often are more abundant in shallow areas where trawling

is impractical. Interestingly, typical slough species (*Leptocottus armatus*, *Platichthys stellatus*, *Phanerodon furcatus*, *Embiotoca jacksoni*, *Cymatogaster aggregata*, and *Hyperprosopon argenteum*) dominated creel census data collected throughout Elkhorn and Bennett Sloughs during our study (Cailliet et al. 1977). As expected from the otter trawl collections, *Psettichthys melanostictus* was commonly caught only by fishermen near the entrance of the slough on the harbor jetties.

Regardless of potential gear biases, Elkhorn Slough is important to several species of fishes as spawning and nursery grounds, as well as a permanent home to at least six resident species. Large numbers of juvenile *Parophrys vetulus*, classified as a marine immigrant, were collected at all stations during the spring and summer months. This commercially important species relies heavily on larger northern estuarine systems as nursery grounds (e.g., Gray's Harbor and Willapa Bay, Washington [Gunderson et al. 1990], Yaquina Bay, Oregon [Pearcy and Myers 1974; Krygier and Pearcy 1986] and Humboldt Bay, California [Toole 1980]), and conspicuously is missing from ichthyofaunal surveys of more southern bays (Horn and Allen 1985). Yoklavich (1982) suggested that Elkhorn Slough is the most southern bay used significantly as a nursery by juvenile *P. vetulus*, and that the occurrence of this species in shallow inshore areas may be limited by ontogenetic changes in thermal tolerance.

Most other flatfish species, including *Citharichthys stigmaeus*, *Paralichthys californicus* (California halibut), and *Platichthys stellatus*, also were considered marine immigrants and occurred as juveniles in larger numbers at the stations closest to the entrance to Elkhorn Slough. All *Sebastes*, which are viviparous marine fishes that spawn offshore, occurred only as juveniles at the near-ocean stations. Spawning *Porichthys notatus* (plainfin midshipman) were relatively abundant in Bennett Slough and at the Kirby Park station in Elkhorn Slough during the spring, and their young were abundant especially in protected areas of Bennett Slough. At least seven species of embiotocids released live young in the slough; three species (i.e., *Cymatogaster aggregata*, *Phanerodon furcatus*, and *Embiotoca jacksoni*) were among the dominant species and were classified as residents and partial residents. Several viviparous species of elasmobranchs, categorized as partial-residents, occur almost year-round and spawn in Elkhorn Slough (Talent 1985). Egg masses, larvae and juveniles of *Clupea pallasii* and the family Atherinidae were abundant seasonally in Elkhorn Slough (Ruagh 1976; Yoklavich et al. 1992), despite the likely underestimation of adult abundance.

The distinct seasonal distribution and abun-

dance of several species can be attributed largely to their reproductive habits. Time of spawning influences the spatial and temporal coincidence of larval and juvenile distributions in the slough. The increase in abundance of juvenile *Clupea pallasii* in upper areas of the slough during spring is consistent with spawning on eelgrass in bays and estuaries along the central California coast during winter months (Miller and Schmidtke 1956). The high abundance of the three dominant species of embiotocids (*C. aggregata*, *E. jacksoni*, and *P. furcatus*) in summer and early fall reflects their summer spawning (Antrim 1981). Their microdistributional patterns within the slough also are related to their reproductive habits, with *C. aggregata* (the numerically dominant species in Elkhorn Slough) entering upper areas of the slough to spawn (Barry 1983) and *P. furcatus* (third dominant overall) spawning at the lower stations (Antrim 1981). *Embiotoca jacksoni* (fourth dominant species and classified as a resident) concentrated as adults and juveniles in the main channel of the lower slough, although both were collected in low numbers at the shallow upper slough stations. Notably, *E. jacksoni* occurs on shallow rocky reefs off southern California (Hixon 1979; Schmitt and Holbrook 1990), but is considered a member of bay and estuarine ichthyofauna closer to its northern geographical margin (Fort Bragg in northern California).

The winter decline in fish abundance and species richness can be attributed to many of the partial-resident species leaving the slough during this time, including *C. aggregata*, *T. semifasciata*, and young *Myliobatis californica*. Notably, this decline occurred during years of relatively normal rainfall (1974–1975) and virtually no rainfall (1975–1976). The resident species that remain in the slough throughout the year are generally euryhaline fishes. Higher dominance indices in winter in Elkhorn Slough are not consistent with results from studies in southern California bays, where high summer dominance coincided with increased abundance of a few species of migratory fishes (e.g., *Engraulis mordax*; Allen 1982; Horn and Allen 1985). In Elkhorn Slough, the trend toward higher dominance indices in the winter, especially in the tidal creeks, reflects the high number of young *Leptocottus armatus*; this resident species spawns in the winter in Elkhorn Slough, and larvae are abundant throughout the slough (Yoklavich et al. 1992).

The role that estuaries and bays play in the life cycle of coastal marine fishes is difficult to assess. The high relative abundance of marine-related (i.e., marine, marine immigrant, and partial-resident life style categories) individuals and species entering Elkhorn Slough early in life or as spawning adults demonstrates the importance of this habitat to

nearshore fish communities. Relatively large numbers of marine immigrants, especially in the highly productive shallow tidal creeks and upper areas of the slough, can function to transport energy from nursery habitats to offshore waters. The occurrence of few habitats such as Elkhorn Slough along the central California coast implies that remaining areas are important to the success of nearshore marine fishes.

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